THE NATURE OF THE MIXED COMMUNITY

By
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The Community as a Set of Individuals

The zoologist's conception of the single-species community is largely based on behaviour. It is because a complex pattern of behaviour links a certain set of individuals of the same species, and distinguishes them from others outside the set, that the set constitutes a community. Consequently this type of community does not occur in the plant world - nor indeed among sedentary animals, or animals whose mobility is mainly passive. It is true that Braun-Blanquet (1951), for instance, refers to the "gregariousness" of a plant species, and describes different species as occurring in "herds", "crowds", etc.; but in fact this refers only to the degree of aggregation of the individuals, and not to any interrelations among them. In general, such aggregations are the result simply of the methods of reproduction and environmental requirements of the species. There may be instances where there is a positive density effect on plant growth - where, up to a certain point, proximity to other individuals of the same species has a favourable effect - but I know of no case where this has been demonstrated apart from nurse-plant effects on seedlings, where the nurse-plant is only fortuitously of the same species. Thus, we may conclude that single-species communities have no real meaning to the botanist.

There are cases where behaviour patterns linking particular individuals of different species enable a multi-species community of animals to be recognised in the same way as the single-species communities already mentioned. Outstanding examples are provided by man and his domestic animals; and in parasitism and commensalism one often finds a persisting association between individuals of different species justifying recognition as a mixed community. In so far as a community in this sense is based on behavioural patterns, however, it is again a concept hardly applicable to plants or sessile animals.

For many years, botanists have been applying the term "community" not to a set of individuals which could be shown through their behavioural patterns to have recognisable linkages, but to a set assumed to have linkages as a result simply of their permanent spatial relationship - in other words, the set of plants occurring within a fixed volume of space. This concept has also been adopted by many zoologists, though commonly in relation to particular animal groups only. The biocoenosis is such a "community" including the whole biota - plants and animals - within the spatial limits specified.

It will immediately be evident that this concept of a mixed "community" has little in common with those considered earlier - or, indeed with the use of the word in everyday life. The species inhabiting the same unit of space do not necessarily have any positive relationship with one another. They simply coexist, perhaps fortuitously, perhaps despite some measure of incompatibility, but certainly without providing evidence, *ipso facto*, that real community relationships between them exist.

The Community as a Set of Species

An alternative to the outlook described in the preceding paragraphs is to regard a mixed community as being constituted by a set of species rather than of individuals. This provides a point of view that can be common to zoologist and botanist. From this point of view, the recognition of a mixed community depends simply on the joint occurrence of the species making it up. Where, within limited sample areas or volumes, a group of species tend to occur together simultaneously, or within a short time interval, to a greater extent than could be expected by chance if their occurrence were independent, they constitute a community. This is a purely empirical definition, saying nothing of the *raisons d'etre* for this joint occurrence, which as we shall see later may be quite varied.

This concept of the community as a set of species, though in conflict with that of the community as a set of individuals, has much to commend it. For one thing it has greater permanence. Any set of individuals is only as permanent as its most short-lived member. And the botanist whose "community" is the stand - the plants growing on a fixed area of ground - has to face the fact that, though his "community" may have temporal continuity, its composition may change completely over a few years, not only in acquiring a new set of individuals, but perhaps even a completely new range of species. The community is thus reduced to a topographical rather than a biological conception.

Moreover, if the community as a set of individuals is held to imply anything more than bare coexistence, demonstrations may be required at every turn that the relationships in question subsist between the individuals and thus constitute them as a community. In principle, such demonstrations are needed for each particular community that is recognised. For a community as a set of species, however, one may regard the demonstration of the community relationships as a once-for-all process.

Finally, if the community consists of all individuals within a specified area, it will usually include many species with no more than a chance association, and by including them in the community its true biological relationships may be obscured. The community as a set of species seems to have more promise in interpreting the current interrelations among them, and between them and their environment, and in assisting the consideration of their evolutionary development, than the community as a set of individuals.

A Geometrical Model

It will facilitate the following discussion if we introduce here a geometrical model which will be commonplace to some of the audience, but new to others. Let us represent the organisms present in any sample area or volume by a point in a multidimensional system in which each axis represents a species. Then the existence of communities in our present sense implies that the points will be concentrated around certain vectors in this space, these vectors being the geometrical representation of the communities. In other words, the points will not be distributed in a hypersphere, with density falling off equally in all directions from a single centre, but in a hyper-ellipsoid whose elongated axes are the vectors spoken of, representing the communities. In two dimensions it is impossible to represent such multidimensional relationships adequately, but Figure 1 may help the reader to appreciate them. Each diagram may be considered as the projection on a plane including two of the species axes of a cloud of points representing the individual sample areas. In Figure 1a the two species are associated in a community, and the line drawn in the figure is a projection of that community vector; species B is more closely associated with it than species A. Where as in Figure 1b, the slope of the vector is negative, it implies that the vector represents two different complementary communities which tend to replace one another in different sites, species A being a member of one and species B of the other.

It has often been said that study of stands in terms of the species they contain, and study of species in terms of the stands in which they occur, are logically equivalent - the geometrical model in one case would have points representing stands in a framework of species coordinates, in the other points representing species in a framework of stand coordinates. This formal equivalence may seem superficially to make biological sense as long as only the presence or absence of the species is considered; but when some measure of quantity of each species in a stand is introduced the apparent equivalence disappears. One can represent different quantities of a given species by distances along an axis. But to do the reverse and allow the distances along a particular axis to represent the quantities of different species in a particular stand would for most biological purposes be meaningless, since the quantities of different species are incommensurable - in general, one cannot say that two individuals of species A are more or less than five individuals of species B, or even that a 50% cover by species C is less than a 70% cover by species D. This becomes even clearer where different measures of quantity (herbage weight for grasses, stem volume for trees, say) have been used for different species. Incommensurability between species is no drawback to the study of interspecific correlation, but for the inverse approach can be surmounted only by some such device as standardization of the variable for each species.

Classification of Mixed Communities

The community as a set of species is one way of generalizing description of the distribution of organisms - of simplifying the bewildering complexity of raw records. Another is by classification of the stands or sets of individuals considered as elementary communities in the other approach. Classification depends on the recognition of groups of stands (or sets of individuals) within which the stands are more similar to one another than they are to stands outside the group. Judgement of similarity for this purpose has most commonly been based on specific composition. The need for classification seems to have been felt more strongly by botanists than zoologists - perhaps because cartography is more important to those who deal with sessile organisms, and cartography becomes much easier if the map can be divided into discrete patches, distinguished by different colours or shading.

In our geometrical model, classification consists in dividing the system into cells by hypersurfaces, all the stands represented by points in one cell being allotted to the same unit of the classification. This method of simplifying the data of species distribution seems to call for discontinuity. Where clusters of points representing stands - Poore's (1955)

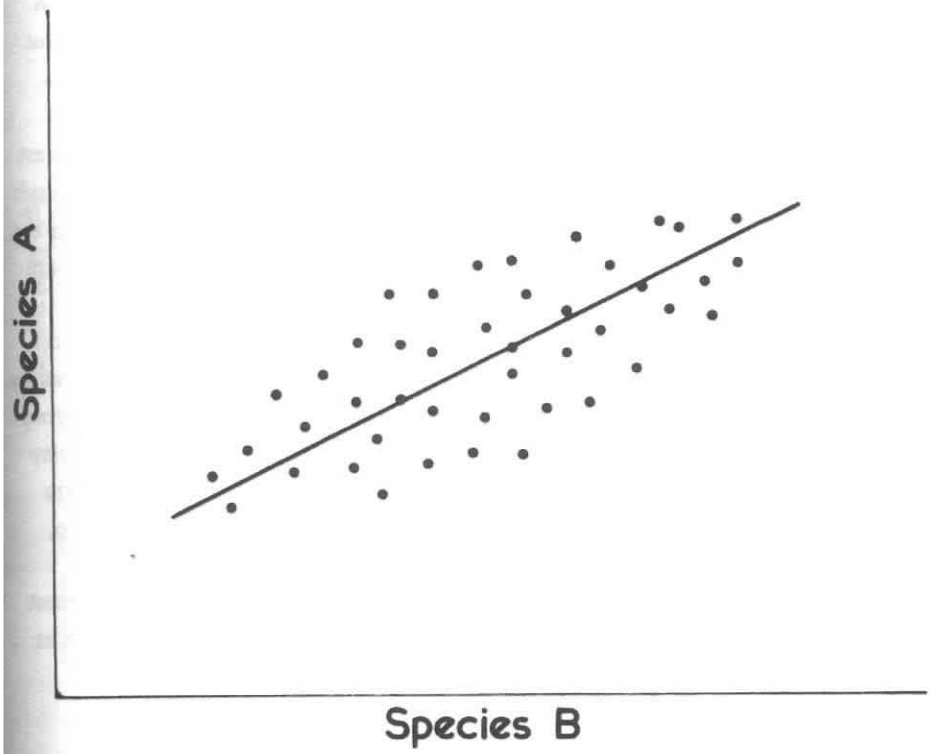

Fig. Ia

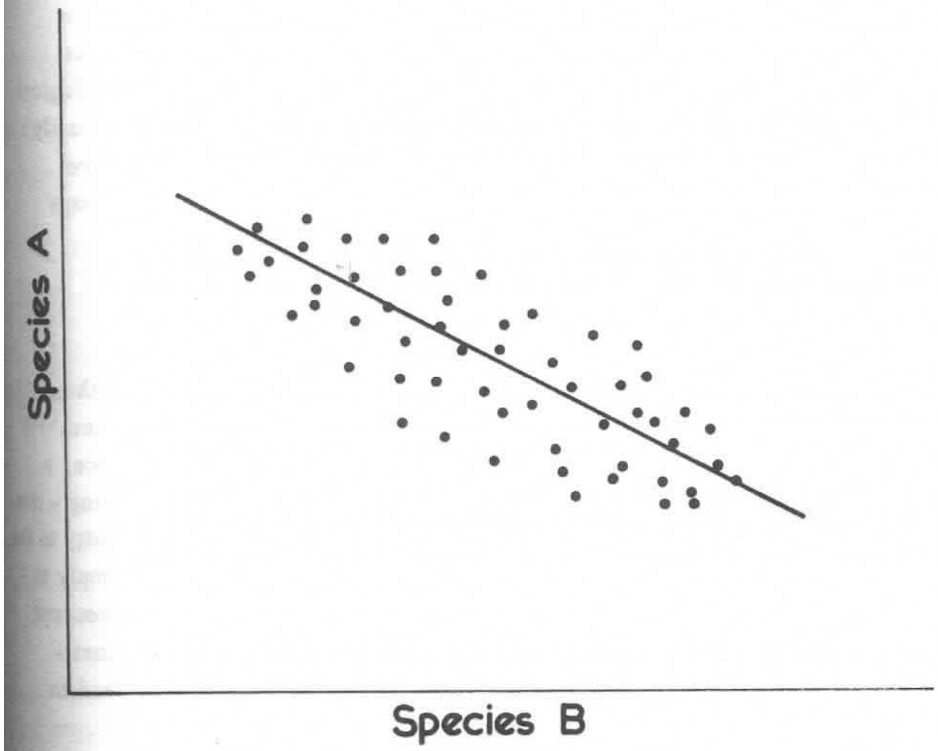

Fig. Ib

noda - are separated by zones of lower density, natural grounds for classification exist. In Figure 2a this situation is presented in a two-dimensional simplification. Species A and B are associated with the same community, represented by the full-line vector; but the majority of samples have either high values for both or low values for both. Consequently one may demarcate two classes of vegetation by drawing the dashed line at right angles to that joining the centres of the two clusters, and through the zone of lowest density between them. Unless such discontinuities occur, there are no objective grounds for distinguishing classes at all. How commonly such natural discontinuities occur in the distribution of points in species-space has been widely discussed. To demonstrate them unequivocally is not easy; and even if they have been found to exist, there may be ambiguities in their interpretation, as will be shown later. Of course, even if the distribution of points appears continuous, zones of species-space could still be demarcated by arbitrary boundaries for purposes of convenience, as in Figure 2b. But the species-group concept of the community does not call for such arbitrary demarcation; the community here is represented not by a cluster of points but by a vector round which the points are assembled. Here, the closeness with which each species is associated with the group, represented by angle between vector and axis, can vary continuously. There is no reason in principle why there should not be a continuous gradation from the species most closely associated with the others of the group to those showing no association with it at all. There may be a discontinuity among the species, but this is not conceptually necessary to a community envisaged in this way.

Another distinction between these two conceptions of the community is that classification of stands virtually excludes the possibility of overlap. Perhaps the whole of the system may not be allotted to classes, so that transitional zones are left between the named cells of the system. But the possibility of a stand belonging to more than one class is not envisaged. On the other hand, when communities are considered as species-vectors, overlap will probably be normal. Though the rather similar "ecological groups" of Ellenberg (1954) and other European writers are usually envisaged as mutually exclusive, this is by no means a necessary feature of this outlook, and it seems more natural to regard each species as associated more or less closely with several - perhaps all - of the vectors recognised.

Sampling of Mixed Communities

A practical point about the recognition of stand-class communities is that the identification of discontinuities will depend entirely upon the range of samples taken. If the difference between stand-classes rests on an underlying environmental difference, a chance lack of intermediate environmental values in the sites selected for sampling - due perhaps to an edaphic discontinuity - might lead to the appearance of a discontinuity in the vegetational data not inherent in the interrelations among the species, but due simply to the sites available for sampling. The same does not apply to the species-group concept. Provided each vector is represented - for preference, including some extreme values - there seems no reason why the inclusion of a discontinuous range of sites should lead to spurious results.

There is another way, however, in which the range of samples will affect the

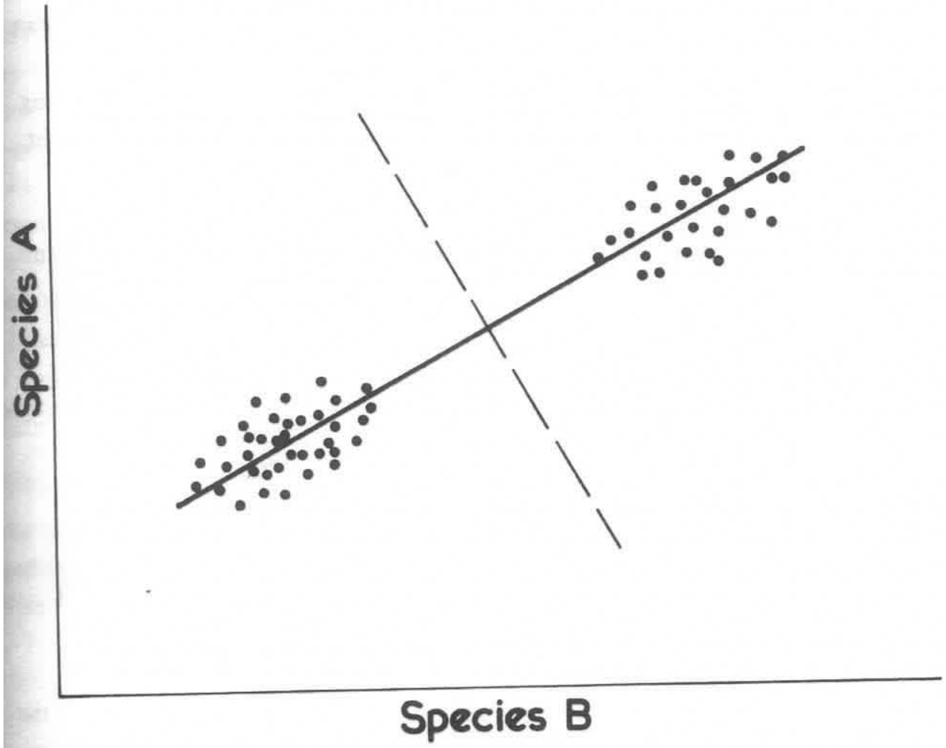

Fig. 2a

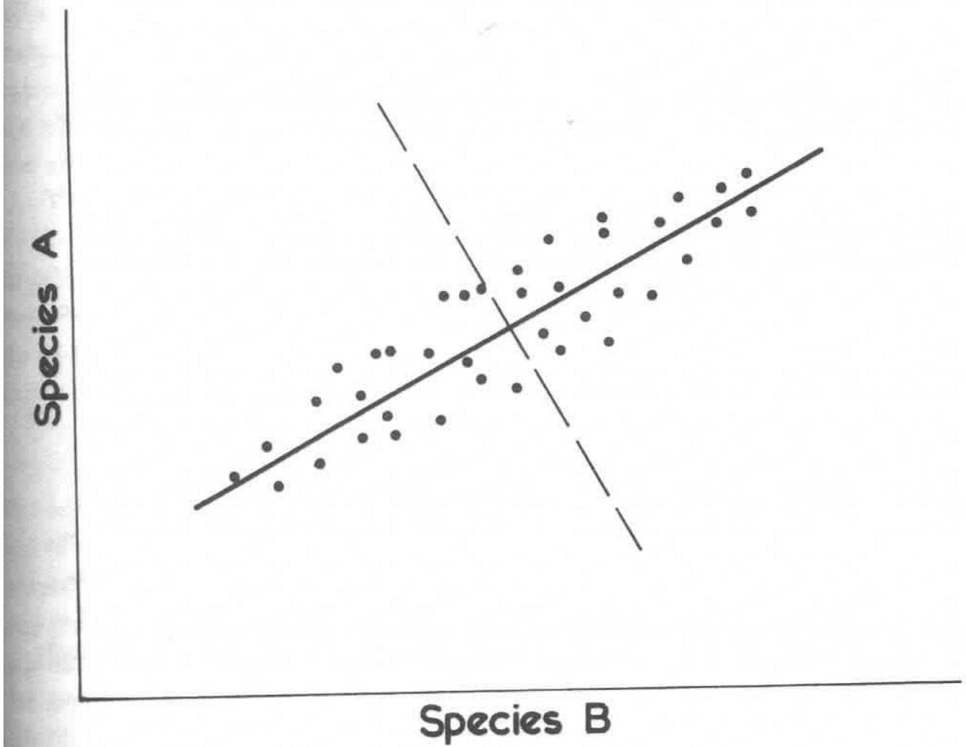

Fig. 2b

recognition of communities whichever approach is adopted. If only a limited range of one of the community vectors is covered, it may well fail to be identified; and the same will also apply to any clusters of points inadequately represented in the sample. In general, mixed communities can only be recognised within the context of the sampling procedure adopted. Sampling more widely is likely to bring new communities to light, or to show that communities already distinguished are in fact sub-sets with the same super-community. Sampling more intensively may lead to the separation of communities already recognised - to the recognition of natural divisions in clusters of points, or to the distinction of two vectors lying close together.

The questions of principle discussed so far apply to mixed communities either of animals or of plants - and indeed might just as well be applied to the joint consideration of both kingdoms in biocoenoses.

Types of Interspecific Relationships

Now, what forms may the interspecific relations take that constitute a mixed community?

(a) Mutual dependence - where the presence of each species is a pre-requisite to the occurrence of the other. Examples of this are few. The best examples might be of the algal and fungal partners in lichens, except that the symbiosis has here gone so far that the partners are not normally recognised as distinct entities. A similar relation is that between the cellulose-digesting higher animals and their gut microflora. Entomophilous plants and their pollinators sometimes provide another example.

(b) One-way dependence. This is a much commoner situation, including all obligate parasitism - and indeed almost all heterotrophic nutrition. In many situations the legume-Rhizobium relationship may fall into this category, and it may include some instances of commensalism. Many epiphytes are entirely dependent on the support provided by their host tree.

(c) Mutual advantage. There are some cases where two species or groups of species improve their performance mutually without being mutually essential. This is probably the case with most mycorrhizal associations, and with the relation between fruit-eating animals and the plants whose seeds they thus disperse.

(d) One-way advantage. Facultative parasites reap advantage from the presence of their hosts, omnivorous facultative predators from the presence of their prey. Zoochorous plants benefit from the animals which carry their seeds on the surface. Plants whose seedlings require protection benefit from the presence of suitable trees and shrubs as nurse plants, and those unable to compete effectively in high light intensity benefit from the shade case by taller species.

(e) Mutual dependence on environment. Finally, the joint presence of two species may not depend on their direct relationship at all- but simply rest on their joint requirement for similar conditions in the inanimate environment.

In the last case one can clearly speak of no specific relationship among taxa - a very large number of species may be included in the same mutual relation with the same complex of environmental factors, differing in the closeness with which their presence or performance is thus determined, and the values of optimum and range for the environmental factor. In all other cases however - where the relation between taxa is a direct one - the question of specificity arises. Where a species is advantaged or completely dependent, is the other member of the relationship a single particular species, or is it a group of species similar in this respect, any of which may replace the others vicariously? In the majority of cases the latter applies, but it is not difficult to find examples of highly specific relations - the rust requiring a single species as host, the insect with a single species of food plant, the legume needing a single species of Rhizobium for effective nodulation.

A community as envisaged here consists, then, of a group of species tending to be found in the same location because of the special environmental features there, together with another group of "hangers-on" not necessarily favoured by the non-living environment, but by the presence of one or more of the first group of species.

The Evolution of the Mixed Community

What part has evolution played in the development of the pattern of the mixed community as we see it today? In the first place, it is clear that evolution in the usual sense is a concept irrelevent to the community envisaged as a class of similar stands. These stands are independent of one another, have no genealogical relationship, do not necessarily have any persistence. On the other hand, the community envisaged as a collection of species may evolve in a real sense. The species of which it is composed change, and as they change the vector in species-space representing the community may change too. One may get some species loosening their association with the group as a whole, others becoming more closely linked. New species may come into the area and enter the group.

But these evolutionary changes which the mixed community undergoes are so far only reflexions of the changes in the individual species making it up. To what extent will these changes have been influenced by the mutual interrelationships among the species? To what extent will the species of the community have undergone a process of mutual evolution?

Wherever a species occurs in several ecotopes, selection will tend to increase its adaptation to that ecotope in which the largest proportion of its population occurs - one of larger extent than the others, or more favourable to this species, or both. Once adaptation to this particular ecotope has begun, the process may be self-accelerating. Any process, in fact, which increases the relative concentration of an organism within a particular part of its potential range will increase the selection pressure exercised by the special features of that part, whether animate or inanimate. A vulnerable animal inhabiting only rock pools is likely to develop crevice-entering behaviour more quickly than one found equally on rocky and sandy shores. And similar processes will operate on adaptation to other species occupying the same ecotope.

The process of adaptation to a specific ecotope - including the other species occurring there - is constantly being opposed by counter-pressure against excessive specialization through the broader evolutionary disadvantages entailed:- the limited population possible, and the greater risk of catastrophe with specialization. The degree of specialization ultimately shown reflects a balance between these opposing pressures, the position of equilibrium depending on such factors as the extent of the favoured ecotope, its degree of differentiation from others, and the extent and frequency of environmental fluctuations.

Only when two species are in a relation of specific mutual dependence or advantage can one consider their mutual evolution as needing no further demonstration. The existence of communities as defined above cannot be taken as proving that mutual evolution has occurred. Clearly the fact that a group of species is associated in this way does not necessarily imply that they have evolved together - they might conceivably have evolved in complete isolation, come together by chance, and then been favoured by the same environmental complex. But most commonly all or many of the species will have been in contact in similar ecotopes during their evolution over the past millenia, and each has contributed to the environment to which all the others have become adapted. This does not by any means imply that the presence of one species of the group is an advantage to the others - the relation may be rather one of mutual toleration. It does imply that the presence of the various species is mutually consistent, and that each species finds at least a local optimum in the particular ecotope where the others also find a local optimum, taking into account the probable population density of each of the other species in the various ecotopes; this overall local optimum may be either in spite of or because of the presence of the other species, or their presence may be irrelevant.

It is now a commonplace that a local optimum, given the presence of other species in the area, may be completely different from the absolute optimum in their absence. It often happens that, in its most favourable environment, a species is repressed or excluded by competition from other species, whereas its wider latitude enables it to colonize other habitats outside the range of these competitors - often in some respect marginal. In a stable situation, where the proportions of the various ecotopes available have remained constant over the centuries, the simultaneous evolution of the species has taken account of these proportions and of the competitive capacity of the various other species with which they may come into contact. The adaptive process will then have led, in each genetically discrete population, to that genetical composition which, over the whole set of ecotopes and in the presence of all the other species populations, enables the maximum number of individuals to survive and reproduce. Thus all the other species present may have influenced the evolutionary process - both those which occur in the same ecotope, and those occurring mainly in other ecotopes from which the species under consideration is excluded. It is very much open to question, therefore, whether the particular group of organisms found together in the same ecotope can properly be regarded as having undergone a process of mutual evolution. In a limited sense, it is true; but the process of mutual evolution extends much further, drawing in all those species capable of existing on the same sites in the absence of competition, and even all species whose zone of tolerance can be linked with that of the species under consideration by one or more species with overlapping zones of tolerance. In fact, linkages can be conceived which associate the evolutionary process for all genetically distinct populations within a continuous land mass, or volume of water.

Once the adaptation of a species has reached a point where most of its individuals occur within one ecotope or a small group of related ecotopes, other species not occurring in these ecotopes can have little influence on its evolution, and adaptation will be in the main to the other species of the same ecotope. But the evolution of these others will also be affected by other species with which they come into contact elsewhere, and only when the whole community is isolated from others will species not belonging to it cease to have an effect on the course of its evolution.

The remarks of the preceding paragraphs are to be interpreted equally in terms of positive advantage afforded by one species to another, and diminished disadvantage such as that arising from the more favourable competitive situation in the favoured ecotope. In this case, likewise, special adaptation to fellow-species in the ecotope where the largest overall population is found is likely to occur, and this special adaptation will progressively increase the preponderance of population in the favoured ecotope up to the point where the disadvantages of specialization reach a balance. Unlike adaptation to the inanimate characteristics of an ecotope, the features to which adaptation is here taking place will themselves be changing progressively, and this may even lead to a change from one favoured ecotope to another. Thus adaptive changes in one species may lead to another species changing its dominant ecotope, and its evolution consequently coming under the preponderant influence of a different set of species.

Thus it can hardly be denied that there will be some measure of mutual adaptation among the species making up a community - and not only where specific relations of advantage are involved. But each species will adapt mainly to the other species encountered by the largest proportion of its individuals, and in general these relationships of strong influence between species will not be two-way. The Russians have a word "edifikator" introduced it seems by Sukachev (1925), which has not yet attained general currency in English-speaking ecology. It is however a useful concept, implying a species which has a strong influence on the environment for the other species of the community, and not necessarily synonymous with a "dominant". It is the edifikators of a community to which the other species finding their largest population in that community may adapt. But the edificators themselves may well be present in larger numbers in some quite different community, and their evolution will then be largely unaffected by the other species of the first community.

The "individualistic" community

Mutual evolution of species in a community has been largely discounted by many advocates - especially among plant ecologists - of the individualistic association; this point of view, associated initially with the name of Gleason (1926), implies the independent response of each species to the inanimate environment, so that the presence together of a particular group of species depends not on their interrelationships, but simply on them happening to have a common environmental optimum. Ecologists adopting this attitude would not deny that environmental conditions can be modified by some of the species present, which thus affect the probability of encountering others. But these modifications, and the resulting effects on other species, are not considered as specific; they might in principle be mediated by any of a large group of species occurring in quite a variety of conditions. Thus, the fact that Neottia occurs mainly in beech forests may not, they would say, be due to any specific adaptation of Neottia to beech, but rather to the fact that it requires shade and leaf litter (which could equally be provided by alder or oak) and, besides this, is favoured by high pH which also favours beech.

It is extremely difficult to devise any critic-proof test of the truth of this hypothesis in a particular case. In fact, it may be doubted whether the hypothesis can be phrased in a precise enough way to make a test possible. Clearly, except where direct relationships such as predation or parasitism are involved, the influence of one species on another can only be through the inanimate environment. Consequently, if the latter were considered in sufficient detail the whole of the influence of one species on another might be accounted for no matter how closely they had evolved together.

It might be thought that the presence of a vector in species-space around which points are concentrated - of groups of species closely associated - might itself be evidence of their mutual evolution. But if the different ecotope conditions are thought of as represented by points in an ecotope-space where the different environmental variables provide the axes, each concentration of points, or mode, in this space is likely to be occupied by a group of species adapting themselves to this ecotope in preference to others, so that every such mode may be expected to be associated with a vector of concentration in species-space. On the other hand, any favoured species-space vector not associated with an ecotope-space mode would be difficult to interpret except in terms of mutual evolution of the species thus associated. This suggests a possible means of test, a positive result of which would certainly be suggestive of mutual evolution. Unfortunately, however, the relevant time for the mutual evolution would lie many years in the past, and there could be no guarantee that the distribution of ecotopes was the same then as now.

Another possible approach to this problem might lie in a study of the nature of boundaries or transitions where one community gives place to another. The hypothesis of mutual evolution would lead one to expect the two groups of species to behave consistently, all those of one group disappearing as those of the other group collectively took their places. It has often been claimed that in vegetational transitions this does not happen - that different species reach their optimal development at different successive points along the transition. A similar approach would consist in plotting the distributional zones of each species in ecotope space and testing whether there was a tendency to coincidence or concentricity. If not, it would be convincing evidence for the individualistic association. But if distributions were concentric it would not answer the question as to whether there had been mutual evolution, or merely adaptation to modal ecotopes. The distinction is a real one, but does not seem to be decidable in any practical case, except perhaps in experimental populations.

Mosaics in Space and Time

So far, we have been considering the ecotope as uniform and undifferentiated. Often this is not so. It may consist of a more or less patterned series of micro-habitats, quite distinct at least for some of the species forming the community. Obvious examples are the bogs of higher latitudes where hummocks and hollows alternate, with different conditions and different species complements for the two elements of the mosaic. Another type of example is provided by forests, where the tree trunks provide ecotopes permitting the growth of bryophytic epiphyte communities absent from the interspaces. Here the ecotope may be uniform for one set of species, quite heterogeneous for another set. If the biocoenosis is viewed on the small scale, different communities will be distinguished which on the larger scale form parts of a super-community.

Often the differentiation of the ecotope is temporal rather than spatial. The species occurring may vary with the season, with the time following fire, or with the course of other cyclical changes. In the limnological and microbiological fields this temporal patterning of mixed communities is commonplace. Often such changes are called "succession", and the communities occurring at different times are treated as distinct. But here as in spatial patterning it is to be questioned whether the different partial communities can properly be treated separately. They form a complex, repeating itself with some regularity in time or place or both, and in so far as mutual adaptation and evolution has been occurring it will in part have affected the complex as a whole. Even apart from cyclical changes in topography, the species of hummock and hollow in a bog are not independent, however distinct they may be. Each group of species has an influence on the other. Likewise in a successional situation, the evolution of the species of each stage will have taken place with reference to the sets of species occupying earlier and later places in the succession. The fact that a species occurs at a particular stage in the succession reflects its more favourable competitive relations with the other species at that stage than with those before and after; but also it would not occur at that stage if it were not to some extent adapted to the earlier species as predecessors; and even in the wrong direction of Time's arrow adaptation to the species that follow may have played some part, for otherwise the stage it occupies might have been telescoped out of existence. Thus on a priori grounds one would expect mutual evolution to have been involved in the development of a community complex in space and/or time, even though the prospects of demonstrating it seem negligible.

Summary

A mixed community defined as a group of associated species seems a more fruitful concept than the more usual definition as a class of similar stands or sets of individuals. On this basis, questions of discontinuity can be avoided, and species may be regarded as belonging to a number of different communities without inconsistency.

The types of relationship between species leading to the formation of communities are discussed, and it is concluded that the community consists of a number of species whose co-occurrence depends on their similar reaction to environmental factors, together

with other species dependent to a greater or less degree on species of the first group.

The role of mutual evolution in the formation of communities is discussed. Each species has become adapted, more or less, to the other species most influential in its favoured ecotope. But these relations are not necessarily mutual, for the latter species may occur in larger numbers in quite different ecotopes, and will there encounter the strongest influences on their own evolution.

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